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Seasonal timing regulates extreme drought impacts on CO_2 and H_2O exchanges over semiarid steppes in Inner Mongolia, China

Yanbin Hao[a,*], Hui Zhang[b,1], Joel A. Biederman[c], Linfeng Li[a], Xiaoyong Cui[a], Kai Xue[d], Jianqing Du[a], Yanfen Wang[a]

[a] College of Life Sciences, University of Chinese Academy of Sciences, Beijing 100049, China
[b] College of Bioscience and Biotechnology, Yangzhou University, Yangzhou 225009, China
[c] Southwest Watershed Research Center, Agricultural Research Service, Tucson, AZ 85719, USA
[d] College of Resources and Environment, University of Chinese Academy of Sciences, Beijing 100049, China

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ABSTRACT

Climate models predict a substantial increase in the frequency of extreme drought, suggesting subsequent impacts on the carbon (C) and water cycles. Although many studies have investigated the impacts of extreme drought on ecosystem functioning, it remains unknown how the timing of extreme drought within a growing season may affect carbon and water cycling. Here we conducted a 3-year field experiment to investigate the influence of seasonal drought timing on ecosystem carbon and water exchange by excluding rainfall (for consecutive 30 days) during three periods of the growing season (May–June, July–August and August–September) in fenced and grazed sites of a semiarid temperate steppe in Inner Mongolia, China. In the fenced steppe, extreme drought reduced growing-season net CO_2 uptake regardless of drought timing, while in the grazed steppe, early-growing season drought caused relatively larger reductions to net CO_2 uptake than drought imposed later in the season. The effect of extreme drought on evapotranspiration (ET) was similar to that of CO_2 exchange at the fenced site, with consistent reductions of seasonally-integrated ET for all treatments compared with the ambient condition. In contrast, at the grazed site, the response of ET to extreme drought was more variable, possibly due to the absence of litter and greater bare ground. Surprisingly, both gross and net carbon uptake declined with increasing ET at the grazed site, while the fenced site showed the positive water-carbon linkage typically seen in semiarid ecosystems. The different responses of CO_2 and water exchanges for the fenced and grazed sites were regulated predominately by soil temperature and soil water content. Together, our results show that drought timing within the growing season can significantly alter drought impacts on ecosystem water and CO_2 exchanges, and that grazing management may further mediate the response.

1. Introduction

Mounting evidence suggests that extreme drought events will escalate in intensity and frequency throughout this century as precipitation variability increases under global warming (De Boeck et al., 2010; Denton et al., 2017). When drought regimes are considered from an ecological perspective, it is becoming increasingly apparent that seasonal timing of drought is also crucial for determining the terrestrial carbon (C) cycle and its feedback to global climate change (De Boeck et al., 2010; Wolf et al., 2016; Zeiter et al., 2016). Extreme drought events can occur at different temporal scales, inter- and intra-annual, triggering potential variation in biophysical variables (such as plant, soil water etc.) and altering CO_2 exchange between the land and the atmosphere (Dietrich and Smith, 2016; Zeiter et al., 2016; Denton et al., 2017). Many studies have shown that extreme drought events, occurring in a variety of seasons, have profoundly influenced plant growth and functioning. However, the ecological implications of greater intra-season variability of precipitation extremes have received minimal notice, especially concerning variable timing of drought within the growing season, which should have the largest ecological consequences (Knapp et al., 2008; Fernández et al., 2014; Dietrich and Smith, 2016).

The effects of seasonal timing of drought on ecosystem C cycling are poorly understood. Ecosystem CO_2 exchange and storage can be altered by shifting of net ecosystem exchange of CO_2 (NEE), which is

* Corresponding author.
E-mail address: ybhao@ucas.ac.cn (Y. Hao).
[1] This author contributed equally to this work.

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determined by the difference between C sequestration through gross primary productivity (GPP) and release through ecosystem respiration (RE). Some studies of naturally occurring drought have shown that ecosystem CO_2 exchange is sensitive to the temporal variability of drought within the year (Wolf et al., 2016; Zeiter et al., 2016). Droughts arising at different stages of the growing season are expected to have different effects on ecosystem CO_2 exchange. We can argue that if droughts occur during sensitive periods for vegetation growth, seasonal ecosystem photosynthesis will decrease more strongly. For example, under severe drought conditions, high evaporative demand, coupled with limited plant canopy development during the early-growing season, could constrain transpiration and CO_2 assimilation. Furthermore, early-season drought may alter vegetation structure such that the ecosystem requires a long recovery period, even after water stress is alleviated (Jongen et al., 2011). Because vegetation is likely to have developed prior to a mid-growing season drought (DM), we expect plants to better tolerate and to recover more quickly from DM (Paruelo and Lauenroth, 1995; Briggs and Knapp, 2001). In the late-growing season, plants approach senescence and become less sensitive to water stress, reducing drought effects on photosynthesis (Dietrich and Smith, 2016). Despite the potential importance of drought timing as a determinant of ecosystem CO_2 exchange, it remains unclear how extreme droughts occurring at different growing stages affect C, due to a lack of experimental studies under manipulated conditions.

Evapotranspiration (ET), which comprises plant transpiration (T) and evaporation (E) from wet canopy and soils, is an important component of ecosystem water cycling. In water-limited ecosystems, ET is also a good proxy for soil water to drive ecosystem CO_2 exchange after hydrologic losses (Biederman et al., 2016, 2018; Jia et al., 2016. Extreme drought can affect ET through altering transpiration and evaporation. Rajan et al. (2015) found that extreme drought suppressed both E and T due to reduced soil water availability. Therefore, seasonal timing of drought may affect ET indirectly by reducing vegetation capacity for transpiration and increasing the fraction of bare ground (Denton et al., 2017) or directly by limiting soil moisture, which supplies both E and T. However, until now, there have rarely been studies to test how seasonal timing regulates the effect of extreme drought on ecosystem ET.

Most field experiments in semiarid regions have found that GPP has a positive relationship with ET, due to higher photosynthesis associated with higher transpiration. Similarly, net CO_2 uptake is usually suppressed by reduced water availability during drought (Xiao et al., 2013; Biederman et al., 2016; Ferlan et al., 2016). However, other studies have found that photosynthesis and respiration showed similar sensitivity to variations in ET, such that decreased GPP is offset by RE declines (Risch and Frank, 2007; Verma et al., 2005). This uncertainty in the relative responses of GPP and RE makes it difficult to predict generally the impact of drought on NEE. The individual responses of GPP and ET to extreme drought determine variations in water use efficiency (WUE = GPP/ET), a powerful index linking C uptake with water availability across diverse biomes. Both field and modeling results have shown that WUE could increase during water stress due to plant adaption (Xiao et al., 2013; Zhang et al., 2017). However, contrasting results suggest WUE can decrease during drought, when lower leaf area reduces the proportion of transpiration to total evapotranspiration (Scott et al., 2015; Jia et al., 2016). The existing uncertainty in responses of both NEE and WUE to drought highlight the need to explore factors regulating ecosystem response to specific scenarios of future extreme climate.

Ecological sensitivity to extreme climate events are highly variable, ranging from little to minor effects (Jentch et al., 2011; Hao et al., 2017) to strong effects on ecosystem structure and function (Bloor and Bardgett, 2012; Boucek and Rehacge, 2014). Ecological resistance (capacity to resist change [Hoover et al., 2014]) and recovery (capacity of ecosystem function returning to the ambient conditions) depend in part on the magnitude, duration, and timing of extreme climate events. Thus, ecosystem resistance and recovery are critical to understanding the relationship between the disturbance (extreme climate) and ecosystem function (carbon and water cycling).

Inner Mongolia temperate typical steppe is an important, extensive ecosystem covering ca. 4.1×10^7 hm^2 and accounting for 10.5% of the total area of Chinese grassland. Inner Mongolia is an optimal location to investigate the generality of ecosystem responses to projected shifts to more extreme precipitation patterns because precipitation controls the development of productivity and distributions of plant life forms (Bai et al., 2004). In this typical steppe, historically most droughts occur in the growing season (May – September) and sometimes last for a few years (Jin and Ala, 2010; Tong et al., 2017; Hessl et al., 2018). Much of the land area in this steppe is grazed, while a significant portion is fenced to exclude grazing. Here, we conducted a 3-year field experiment of extreme drought events to investigate the potential influence of drought on ecosystem carbon and water exchange during three plant growth stages in fenced and grazed sites within a semiarid temperate steppe in Inner Mongolia, China. Specifically, we addressed the following questions: (1) How does extreme-duration drought affect CO_2 and water exchanges between the land and the atmosphere? (2) Are such responses sensitive to the within-season timing of extreme drought? (3) What are the roles of soil moisture, soil temperature and land management (fenced vs. grazed) in regulating such responses?

2. Methods

2.1. Sites

To evaluate the effect of extreme drought and its seasonal timing on CO_2 and water exchange in steppe ecosystems, we conducted a rainfall manipulation experiment in Inner Mongolia, China during three growing seasons (2014–2016). The sites included a fenced (i.e. not grazed) portion of the Inner Mongolia Grassland Ecosystem Research Station (43° 32′N, 116° 40′E, 1200 m a.s.l.) and a grazed portion of the Joint Research Station of Animal Ecology (44° 11′N, 116° 27′E, 1100 m a.s.l) in the Xilin River watershed of the Inner Mongolia Autonomous Region (Fig. S1). Details for each site are provided below and summarized in Table 1.

Table 1
Location, climate, soil descriptions, vegetative characteristics and manage patterns for the Grazed site locate at Joint Research station of Animal Ecology and the Fence site locate at Inner Mongolia Grassland Ecosystem Research Station in Inner Mongolia steppe, China.

Location	Grazed	Fenced
Latitude, Longitude	116°45'E, 44	116°40'E, 43°32'N
Elevation (m)	1079	1240
Management pattern	Grazed	Fenced
Climate		
MAP (mm)[a]	350	358
MGSP (mm)[a]	280	318
MAT (°C)[a]	−1.4	−0.5
Soil		
Taxonomy	Chestnut	Dark chestnut
Sand (%)	65	60
Clay (%)	18	21
Silt (%)	17	19
pH	8.4	7.4
%SOC	1.1%	1.6%
%TN	0.14%	0.24%
Dominant species	*Leymus chinensis, Stipa grandis, Medicage Falcata*	*Leymus chinensis, Stipa grandis, Agropyron cristatum, Cleistogenes squarrosa, Carex duriuscula*

[a] MAP: mean annual precipitation; MGSP: Mean growing season precipitation; MAT: mean annual air temperature.

The extreme drought treatments were defined by the duration without effective ecological precipitation. We fit a Gumbel I distribution to the 60-year period of available local weather records and determined that the ~60-year recurrence extreme drought had a duration of 30 days. This extreme-duration drought was imposed in one of three seasonal timing treatments including: early (DE, May–June), middle (DM, July-August) and later growing season (DL, August–September). These three drought timings correspond with periods of seedling establishment, growth and senescence of vegetation, respectively.

2.1.1. Long-term fenced steppe (fenced)

The site located at the Inner Mongolia Grassland Ecosystem Research Station has been fenced off to prevent grazing since 1979. It is situated on a smooth wide plain with low hills. The region is characterized by a temperate continental climate with mean annual temperature of −0.5 °C and mean annual precipitation of 358 mm, of which an average of 89% (318 mm) occurs during the growing season (Hao et al., 2010). The xeric rhizomatous grass *Leymus chinensis* is the dominant species, but *Stipa gradis*, *Agropyron cristatum*, *Achnatherum sibiricum* and *Carex korshinskyi* are also common. The grass cluster heights range from 50 to 60 cm, and coverage can reach 80–90% during rainy years. The soil type is dark chestnut (Mollisol) with a depth of 100–150 cm, typical for steppe ecosystems of this region. The A horizon is 20–30 cm deep, and there is no obvious $CaCO_3$ layer in the soil profile. Mean surface soil organic carbon and total nitrogen content are 25.7 and 2.4 g kg^{-1}, respectively (Hao et al., 2010).

2.1.2. Grazed steppe (grazed)

The site in the Joint Research Station of Animal Ecology has been used for grazing from June to October with moderate grazing pressure of ca. 1.5 sheep hm^{-2} before the experiment. Grazing was excluded during the experiment. Mean annual temperature is −1.4 °C. The average annual precipitation is 350 mm of which an average of 80% (280 mm) occurs during the growing season. The grazed site contains fewer grass species than the fenced site, and *L. chinensis, S. grandis,* and *C. squarrosa* are the dominant species. *Artemisia frigida*, *Potentilla acaulis*, and *Chenopodium glaucum* constitute a large proportion of the total number of individual plants, but their biomass only accounts for a small fraction of the total (< 10%). The height of the grass clusters is 20–30 cm with coverage averaging 10–15%. An important contrast between the two sites is that there is almost no litter accumulation under grazing.

2.2. Experimental protocol and design

We manipulated the timing of extreme drought events within the growing season using 16 rainout shelters at each site. The experiment was a randomized block design with four replicate plots for each treatment at each site. During the treatment, ambient rainfall was excluded from the treatment plots (2 m × 2 m) using rainout shelters (3 m × 3 m of height 1.8 m in the fenced site, 4.5 m × 6 m of height 3 m in the grazed site). Treatment plots were isolated from surrounding soils using metal flashing (extending approximately 0.4 m below and 0.1 m above the ground surface) to prevent lateral transfer of soil water. For further details of the rainout shelter design, see Hao et al. (2017). During the growing season each year, shelters were installed and covered the plots during the treatment period and then removed after the treatment. The ambient control plots remained without rainfall manipulation throughout the entire experiment. The timing of extreme drought events is presented in Table S1. At the Fenced site, the extreme drought treatments – DE, DM and DL – reduced total growing-season precipitation by 13–26%, 14–27% and 15–30%, respectively, as compared with ambient. Similarly, growing-season precipitation was reduced by 29%–38%, 8%–25% and 4%–36% for DE, DM and DL at the Grazed site.

2.3. Soil water content and soil temperature

Soil water content (SWC) was measured weekly in the center of each plot at depths of 0–20 cm using 20-cm time domain reflectometry probes (Model TDR 300, Spectrum Technologies, Inc., USA) inserted vertically. Soil temperature (Ts) at a depth of 5 cm below the surface was monitored using a thermometer in the center of each plot (Model TL-883, Tonglixing technology Co., Ltd., China).

2.4. Ecosystem CO_2 and water exchange measurements

Prior to the experiment, a square stainless steel frame (50 cm × 50 cm, 10 cm high) was inserted 7 cm deep in each plot, with 3 cm extending above ground to facilitate gas flux measurements. We used a static transparent chamber method for NEE and ET and static opaque chamber method for RE measurement (for details see Li et al., 2016 and Hao et al., 2017). All flux measurements were completed during the morning (9:00–11:30) on sunny days. Briefly, NEE and ET were simultaneously measured using a transparent chamber (0.5 m × 0.5 m × 0.5 m) attached to an infra-red gas analyzer (LI-840 A, LI-COR Inc., Lincoln, NE, USA) over the steel soil frame. The chamber was equipped with a temperature sensor and two small fans to mix the air, ensuring even gas sampling. A pump (6262-04, LI-COR Inc.) circulated air from the chamber into an infra-red gas analyzer, and the CO_2 and water vapor concentrations were recorded every second for 2 mins. The data for the first and last 10 s were deleted, and NEE and ET were calculated. After measuring NEE, the chamber was lifted and vented, placed back on the frame, and covered by a lightproof cloth to estimate RE (i.e. NEE in the absence of photosynthesis). Gross primary productivity (GPP) was calculated by the difference between RE and NEE. Water use efficiency (WUE) was defined as the ratio of GPP to ET.

2.5. Statistical analysis of impacts on CO_2 and water exchange

To assess the sensitivity of RE and GPP to extreme drought events, the sensitivity is determined as the difference on each sampling date between average CO_2 exchange in the drought plots (CO_2-drought.) and that in controls plots (CO_2-contr.) during (i.e. resistance) and post drought treatment (i.e. recovery) according to Eq. (1):

$$\text{Sensitivity} = \%\ change\ \ from\ \ control = \left(\frac{\overline{CO_2\text{–drought}} - \overline{CO_2 - \text{contr.}}}{\overline{CO_2 - contr.}}\right) \times 100\% \quad (1)$$

Because NEE may take either negative or positive values and therefore switch signs, Eq. (1) is not appropriate for assessing NEE resistance and recovery. Instead, NEE observations for the period of interest were assigned a rank in order of descending value, positive to negative. Therefore, average NEE in Eq. (1) can be replaced with the rank sum of NEE, i.e.

$$\text{Sensitivity for NEE} = \%\ change\ \ from\ \ control = \left(\frac{Rank\ \ sum_{NEE}.\ drought - Rank\ \ sum_{NEE}.\ contr.}{Rank\ \ sum_{NEE}.\ contr.}\right) \times 100\% \quad (2)$$

A negative or positive value of sensitivity means lower or higher *resistance* during the drought and likewise for *recovery* following drought. The statistical significance of the resistance and recovery was calculated from the difference of ecosystem CO_2 exchange between drought and control plots.

Soil moisture, soil temperature, NEE, RE, GPP, ET and WUE for each site and treatment were compared over the whole growing season using

repeated measures ANOVA with the general linear model (PRCO GLM). The three extreme drought treatments were treated as independent variables, and dependent variables included ecosystem CO_2 exchange, ET, WUE, SWC and Ts. When treatment effects were significant, Duncan's Multiple Range Test was used to compare mean values among the treatments. Before conducting an ANOVA, the normality of error terms was evaluated using the *Kolmogorov-Smirnov* test, and data were square-root transformed if errors were not normally distributed. Homoscedasticity was evaluated using the *Levene* test for equality of variances. To illustrate the relative importance of seasonal timing of extreme drought on ecosystem CO_2 exchange, a linear model was used to model the relation between NEE and the amount precipitation, soil water content and drought periods. Two dummy variables of early-season (DE) and mid-season (DM) drought were used in the linear model, with late-season (DL) drought arbitrarily chosen to serve as the reference. All statistical analyses were carried out by using SAS 9.2 (SAS Institute, Cary, NC, USA).

3. Results

3.1. Precipitation and air temperature

During the growing seasons of 2014–2016, ambient rainfall was 205 mm, 229 mm and 165 mm at the Grazed site, and 256 mm, 243 mm and 187 mm at the Fenced site (Fig. 1 and Table S1). Compared with long-term (1952–2013) same-period average values (280 mm for the Grazed, 318 mm for the Fenced), the three study years were relatively drier than the historical averages. The amount of ambient rainfall excluded during the 30-day extreme drought treatments varied from 63 to 67 mm for early drought, 14–57 mm for the mid-season drought, and 9 to 60 mm for the late-season drought in the Grazed site. At the Fenced site, these reductions ranged from 33 mm to 41 mm (early), 37 mm to 52 mm (middle), and 38 mm to 48 mm (late) (Table S1). Air temperatures during the experiment were not significantly different from mean historical temperatures. Peak temperatures occurred in July.

3.2. Responses of soil water content and soil temperature

Extreme drought treatments in all three seasonal periods reduced mean growing season soil water content (SWC) at both sites (Fig. S2 and Table 2). At the Grazed site, mean seasonal SWC was decreased 9%–19% by the early-season drought, 5%–31% by the mid-season drought, 9%–24% by the late-season drought compared with the ambient condition. At the Fenced site, SWC decreased 5%–10% for the early-season drought, 6%–14% for the mid-season drought, 11%–15% for the late-season drought (Fig. S2). When considering only the 30-day drought treatment periods, mean soil water content showed greater reductions ranging from 30% to 70% and 16% to 50% in the Grazed and Fenced sites, respectively (Fig. 2a, b).

Drought treatments were associated with significant changes in mean growing season soil temperature at the two sites over the three treatments and three study years (Fig. S2 and Table 2). At the Grazed site, drought either had no effect or increased growing-season mean soil temperature by up to 3.7 °C, while at the Fenced site, seasonal soil temperature impacts were generally small and mostly not significant (Fig. S2). During the 30-day treatment periods, soil temperature at the Grazed site increased 0.9 °C–3.2 °C for early-season drought, 2.4 °C–3.9 °C for late-season drought in 2014 and 2016, while only *ca.* 0.1 °C for mid-season drought compared with the ambient. However, there were increases of 3.7 °C-3.0 °C for mid- and late-season drought in 2015 (Fig. 2c). At the Fenced site, drought treatments had no significant influence on soil temperature in 2014 and 2015, while there was a significant effect of early-season drought on soil temperature in 2016. Even during the 30-day treatment periods, soil temperature differences were minimal at the Fenced site (Fig. 2d).

3.3. Responses of CO_2 and water exchanges

Drought treatments significantly influenced mean seasonal ecosystem CO_2 exchange (GPP, RE and NEE) and water (ET) at both sites (almost all $P <$ 0.01, Table 2), although the responses differed

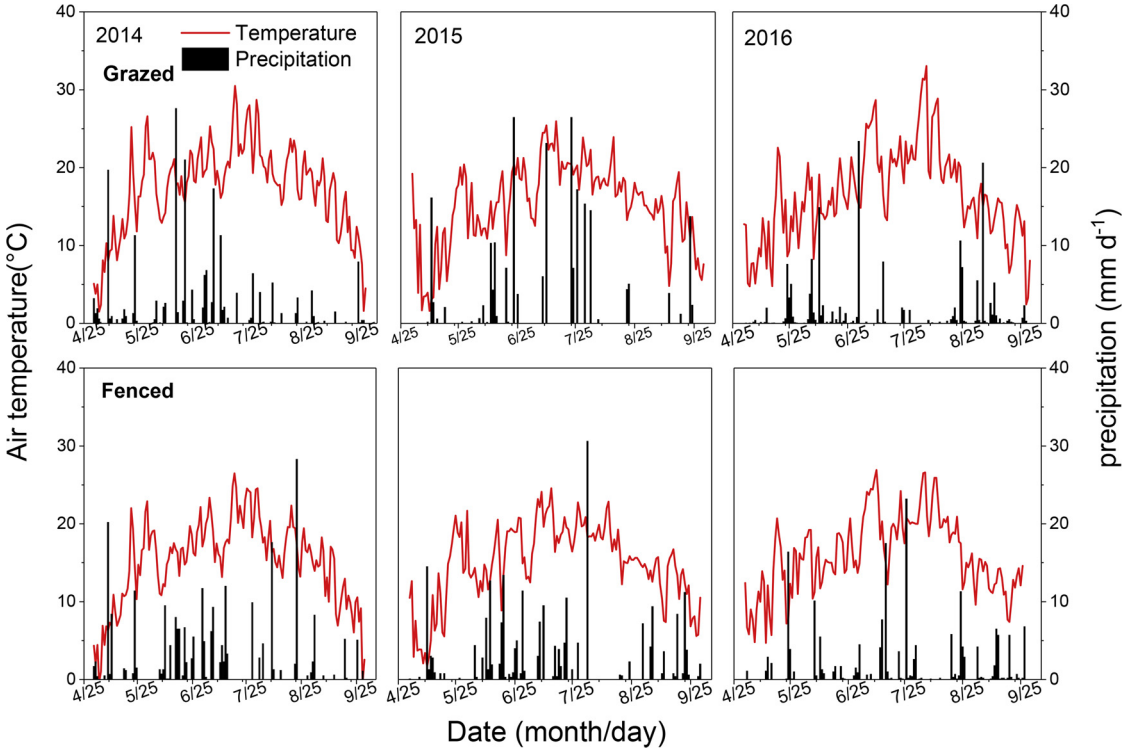

Fig. 1. Mean daily air temperature and total daily precipitation during three growing seasons from 2014 to 2016 in the grazed (Grazed) and fenced (Fenced) steppe in Inner Mongolia Plateau, China.

Table 2
Results of repeated-measures ANOVA for responses of soil water content (SWC), soil temperature (Ts), gross primary productivity (GPP), ecosystem respiration RE), net ecosystem CO_2 exchange (NEE), evapotranspiration (ET) and water use efficiency (WUE) to extreme drought treatments, sampling date and their interaction for the studies year at the Grazed and Fenced sites. *P* values smaller than 0.05 are in bold.

Site	Year	Resource		SWC		Ts		GPP		RE		NEE		ET		WUE	
			df	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Grazed	2014	Treatment(T)	3	9.16	**0.03**	5.24	**0.002**	14.67	< **0.0001**	9.46	< **0.0001**	4.05	**0.009**	9.57	< **0.0001**	3.12	**0.03**
		Sampling date (D)	13	138.21	< **0.0001**	36.73	< **0.0001**	163.46	< **0.0001**	164.39	< **0.0001**	42.6	< **0.0001**	62.47	< **0.0001**	9.99	< **0.0001**
		T × D	39	5.67	< **0.0001**	3.81	< **0.0001**	6.54	< **0.0001**	7.83	< **0.0001**	3.10	< **0.0001**	6.15	< **0.0001**	2.63	< **0.0001**
	2015	Treatment(T)	3	28.25	< **0.0001**	55.38	< **0.0001**	13.20	< **0.0001**	8.92	< **0.0001**	5.71	0.001	7.62	0.0002	4.26	**0.01**
		Sampling date (D)	12	48.61	< **0.0001**	39.69	< **0.0001**	27.10	< **0.0001**	34.57	< **0.0001**	14.27	< 0.0001	16.13	< **0.0001**	4.81	< **0.0001**
		T × D	36	4.62	< **0.0001**	2.16	**0.001**	1.91	**0.008**	2.13	**0.003**	1.84	0.01	1.33	0.17	2.28	**0.001**
	2016	Treatment(T)	3	11.53	< **0.0001**	13.68	< **0.0001**	11.34	< **0.0001**	6.55	0.**0005**	9.16	< **0.0001**	3.77	**0.01**	1.35	0.26
		Sampling date (D)	9	55.05	< **0.0001**	70.23	< **0.0001**	9.60	< **0.0001**	11.90	< **0.0001**	15.40	< **0.0001**	6.96	< **0.0001**	3.38	**0.001**
		T × D	27	5.25	< **0.0001**	3.11	< **0.0001**	2.13	**0.004**	1.27	0.19	4.23	< **0.0001**	1.84	**0.02**	1.09	0.36
Fenced	2014	Treatment(T)	3	15.07	< **0.0001**	1.59	0.19	13.35	< **0.0001**	13.56	< **0.0001**	4.83	**0.004**	6.01	**0.0009**	0.14	0.94
		Sam pling date (D)	11	264.70	< **0.0001**	300.88	< **0.0001**	44.112	< **0.0001**	77.65	< **0.0001**	13.10	< **0.0001**	24.87	< **0.0001**	4.21	< **0.0001**
		T × D	33	12.32	< **0.0001**	0.89	0.64	3.32	< **0.0001**	3.39	< **0.0001**	1.92	**0.008**	1.64	**0.03**	0.84	0.71
	2015	Treatment(T)	3	13.48	< **0.0001**	2.12	0.1	3.36	**0.02**	6.92	**0.0003**	5.93	**0.001**	5.90	**0.001**	2.61	0.05
		Sam pling date (D)	21	93.72	< **0.0001**	651.08	< **0.0001**	63.43	< **0.0001**	132.75	< **0.0001**	21.14	< **0.0001**	76.68	< **0.0001**	10.43	< **0.0001**
		T × D	63	9.67	< **0.0001**	1.2	0.21	12.46	< **0.0001**	3.04	< **0.0001**	1.88	**0.007**	2.17	**0.0019**	1.5	0.07
	2016	Treatment(T)	3	8.21	< **0.0001**	5.9	**0.0009**	7.81	< **0.0001**	5.27	**0.002**	7.64	0.**0001**	8.38	< **0.0001**	3.58	**0.02**
		Sampling date (D)	23	53.60	< **0.0001**	201.9	< **0.0001**	50.04	< **0.0001**	71.45	< **0.0001**	23.83	< **0.0001**	45.22	< **0.0001**	7.92	< **0.0001**
		T × D	69	5.09	< **0.0001**	6.9	< **0.0001**	2.53	< **0.0001**	2.97	< **0.0001**	2.79	< **0.0001**	4.73	< **0.0001**	1.78	**0.014**

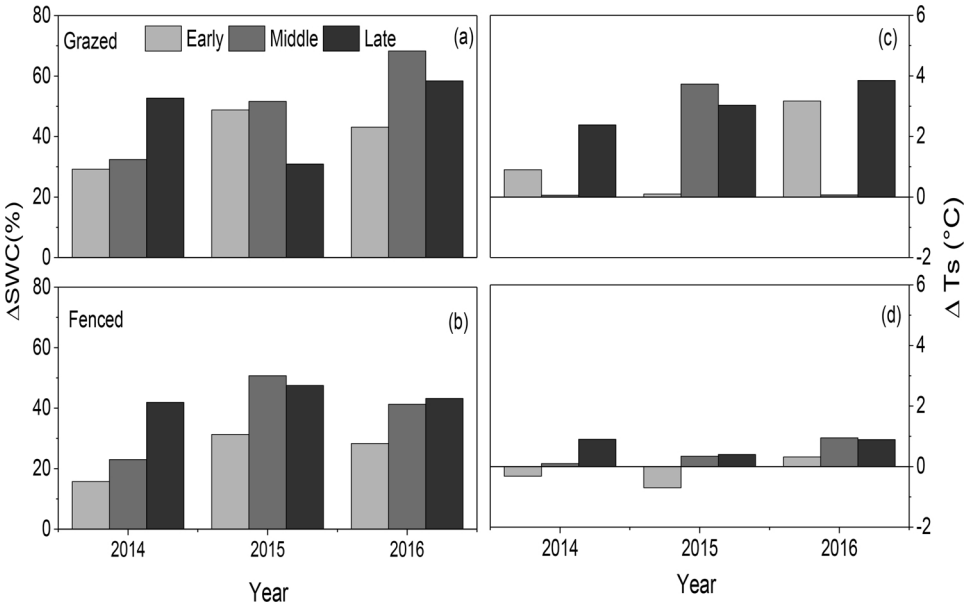

Fig. 2. Percentage (%) difference in soil temperature (ΔTs, 0–5 cm depth of soil) and soil water content (ΔSWC, 0–20 cm depth of soil) between during-drought treatment and synchronous ambient condition at the Grazed (a, c) and Fenced site (b, d). respectively. Treatments: early-growing season drought (Early), mid-growing season drought (Middle) and late-growing season drought (Late).

between the two sites. At the Grazed site in 2014 and 2016, early-season drought significantly increased seasonal NEE, producing average release to the atmosphere of 0.31 and 0.56 μmol CO_2 $m^{-2}s^{-1}$, while the ambient plots were carbon-neutral over the growing season (NEE ~ 0) (Fig. 3a). All plots at the Grazed site were carbon sinks (NEE < 0) in 2015, although mid-season drought reduced the seasonal sink magnitude to less than half of the ambient. Similarly, early-season drought at the Grazed site reduced growing-season GPP, RE and ET in 2014 and 2016, although it increased these fluxes in 2015 (Fig. 3b–d). Seasonal fluctuation of CO_2 and water exchanges was also observed, especially during the 30-day treatment period (Fig. S3). At the Fenced site, all three drought treatments decreased mean seasonal CO_2 and water exchanges across all three study years. The average NEE, RE, GPP and ET decreased by *ca.* 18–35 %, 10–23%, 10–28% and 5–25% for the Fenced site drought treatments compared with the ambient, respectively. However, there were no significant differences in mean seasonal fluxes among the three drought treatments (Fig. 3e–h). Nearly all of the extreme drought events significantly depressed CO_2 and water exchanges during the 30-day drought periods (Fig. S4).

3.4. Sensitivity of ecosystem CO_2 exchange to extreme drought

The sensitivity (resistance during drought period and recovery following drought) of ecosystem CO_2 exchange (NEE, RE and GPP) was negative and mostly significant for drought treatments at the Fenced site, whereas sensitivity varied more widely at the Grazed site (Fig. 4). At the Grazed site, all CO_2 fluxes showed low resistance to mid-season drought across all study years (Fig. 4a–c), while NEE showed low resistance to the early-season drought in all years (Fig. 4c). Grazed-site CO_2 exchange did not recover well after suffering from the early-season drought in 2014 and 2016 (Fig. 4d–f). The Fenced site showed consistently low sensitivity; regardless of the seasonal timing, both the resistance and recovery of CO_2 exchange to extreme drought were negative, indicating low resistance and recovery. Notably, recovery of CO_2 exchange from late-season drought was lower than other two drought treatments (Fig. 4 j–l).

3.5. Effect of removing precipitation on ecosystem CO_2 exchange

The amount of precipitation excluded by a given treatment (ΔP) and consequent variations in soil temperature (ΔTs) have linear positive relationships with seasonal average variations in NEE at both sites (ΔNEE, i.e. the difference of NEE between the drought and ambient treatments, Fig. 5). Furthermore, the slopes of ΔP and ΔTs to ΔNEE (0.04 and 0.69) for the Fenced site were greater than those (0.02 and 0.14) for the Grazed site (Fig. 5a, b), respectively. Interestingly, the variations in soil water (ΔSWC) had a positive relationship (i.e. decrease C sink and/or increase C source) with ΔNEE at the Grazed site and a negative relationship at the Fenced site (Fig. 5c). There was a negative linear relationship of ΔRE with both ΔP and ΔTs, but no significant relationship with ΔSWC (Fig. 5d–f). Meanwhile, ΔGPP showed a negative relationship with ΔTs and a positive response to ΔSWC, but no significant relationship with ΔP (Fig. 5g–i). Multiple regression analyses indicated that at the Grazed site, the negative effect of early-season drought on growing-season CO_2 exchange was greater than for mid- and late-season drought with greater standardized regression coefficients (Table 3). Multiple regression indicated that at the Fenced site, early- and mid-season drought had greater impacts than late-season drought on NEE. However, early- and mid-season drought are equally important in terms of depressing the net carbon uptake (Table 3).

3.6. Relationships of CO_2 and ET with soil moisture and temperature

To explore the greater drought sensitivity of the Fenced site as compared to the Grazed site, we next evaluated relationships between CO_2 and water exchanges as well as the putative drivers soil moisture and temperature. NEE decreased (net CO_2 uptake increased) linearly with the increase of SWC at both sites (Fig. 6), but the sensitivity of NEE to variation in SWC was more than twice as large at the Fenced as the Grazed site (Slope = −0.13 at the Grazed and slope = −0.31 at the Fenced site). Similar patterns were observed for GPP and RE at the fenced site, with positive linear relationships to SWC. At the Grazed site, however, we found no relationship of GPP or RE with SWC (Fig. 6a, d). ET and WUE each increased significantly with SWC at both sites (Fig. 6b, e, c, f). Although the ET slope with SWC was greater at the Fenced site than the Grazed site, the GPP slope increase between sites was even greater, meaning that WUE was more sensitive to SWC at the Fenced site (Fig. 6c, f).

Variations in CO_2 and water exchange were related to soil temperature across both sites (Fig. 7). Although GPP and RE had similar, negative responses to soil temperature increases at the Grazed site, the

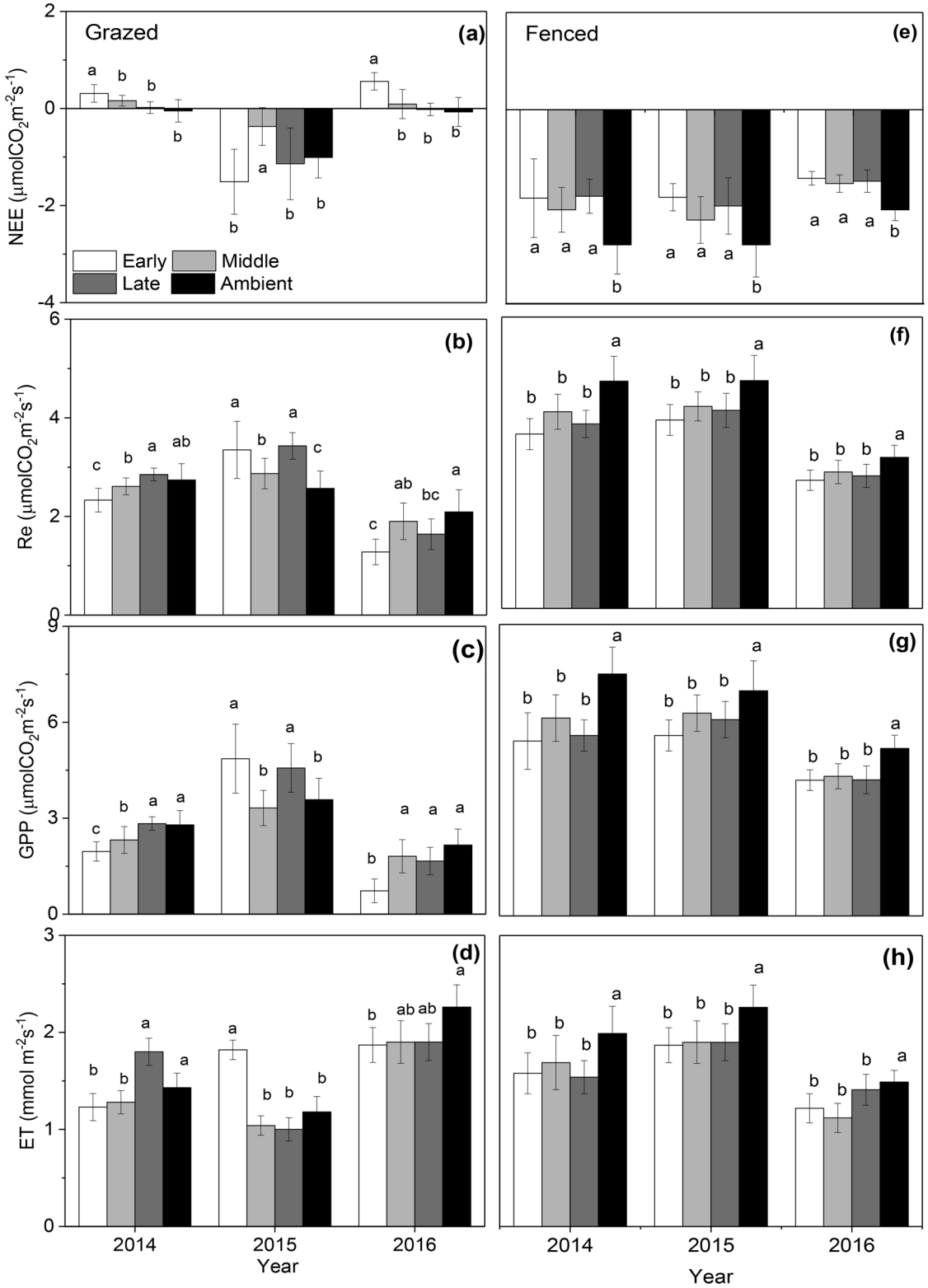

Fig. 3. Mean (± 1 SE) seasonal net ecosystem carbon exchange (NEE), gross ecosystem productivity (GPP), ecosystem respiration (RE) and evapotranspiration (ET) under extreme drought treatment at early-(May to June), mid- (July to August) and late-growing season (August to September) from 2014 to 2016 at the (a–e) Grazed and (f–j) Fenced site. Different letters indicate significant differences of means between treatments at $P \leq 0.05$. See Fig. 2 legend for treatment abbreviations.

Fenced site showed greater temperature sensitivity for GPP than RE, consistent with a positive NEE response. Divergent responses of ET and GPP to Ts caused opposite responses of WUE to soil temperature at the two sites.

3.7. Relationship between CO_2 and water exchange

We found the relationship between water and CO_2 exchange was different at the two sites (Fig. 8). At the Grazed site, there was a marginally significant linear increasing relationship between NEE and ET

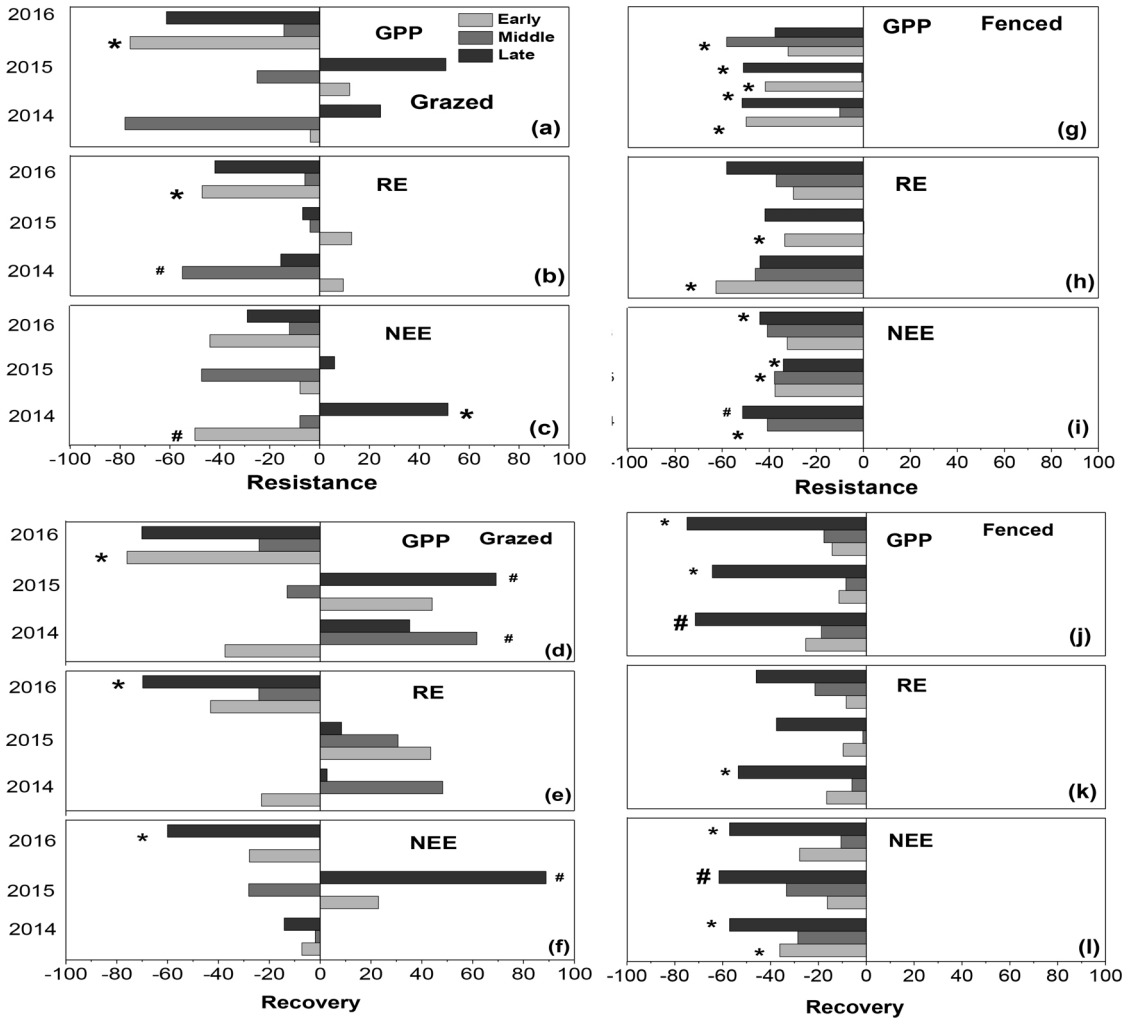

Fig. 4. Sensitivity of (a, g and d, j) gross ecosystem productivity (GPP), (b and h, e and k) ecosystem respiration (RE) and (c and i, f and l) net ecosystem carbon exchange (NEE) responses during-extreme treatments and post-drought treatment at the Grazed and Fenced sites. Sensitivity is a dimensionless parameter (Eqs. (1) and (2)). See Fig.2 legend for treatment abbreviations. * and # means significant at $P \leq 0.05$ and $P \leq 0.01$ respectively.

($R^2 = 0.1$, $P = 0.1$) with a slope of 0.35 μmol CO_2 mmol$^{-1}H_2O$, consistent with GPP and RE showing similar slopes with respect to ET (Fig. 8a). In contrast, the Fenced site showed a negative relationship between NEE and ET ($R^2 = 0.6$, $P < 0.01$) with a slope of -0.95 μmol CO_2 mmol$^{-1}H_2O$. This larger, negative slope results from the greater sensitivity of GPP (Slope = 3.0) than of RE (Slope = 2.0) to ET (Fig. 8b).

4. Discussion

During a three-year rainfall manipulation experiment in the Inner Mongolian steppe, extreme-duration drought (30 days) reduced the gross and net carbon uptake of a grazed site only when the drought occurred early in the growing season, whereas net carbon uptake was reduced at a fenced site regardless of when the drought occurred. Similar impacts were observed for ET. Stronger responses in the fenced ecosystem resulted from greater sensitivity to soil moisture and temperature. Below, we discuss how extreme-duration drought, within-season drought timing and land management regulate land-atmosphere exchange of carbon and water, and implications for carbon cycling of semiarid grasslands.

4.1. Does extreme drought decrease ecosystem CO_2 and water exchange?

During the growing season, a 30-day extreme drought event caused a significant decrease in net carbon uptake from the Fenced site, and significantly negative or no effect on CO_2 uptake (negative NEE) at the Grazed site (Fig. 3) due to the differential sensitivity of GPP and RE during and post-drought treatment (Fig. 4). Drought-reduced SWC (Fig. 2) caused larger reduction in GPP than in RE (Fig. 6), thereby reducing the magnitude of NEE. It has been previously shown that many ecosystems experience reductions in net carbon uptake during water limitation because GPP is more sensitive than RE (Niu et al., 2008; Schwalm et al., 2010; Zhou et al., 2013; Biederman et al., 2018). However, antecedent SWC status also has important effects on the response of GPP and RE (Hao et al., 2010; Law et al., 2003). When antecedent SWC is very high, drought treatment can initially stimulate GPP more than RE, enhancing NEE (more uptake) if short-term drought reduces soil moisture and/or increases soil temperature into optimal ranges for plant growth. For example, considering the early-season drought in 2015 at the Grazed site, higher antecedent SWC associated with greater precipitation in advance of the growing season (Fig. S2) resulted in greater net carbon uptake during drought as compared to ambient (Fig. 3), although the difference was not significant. It is worth noting that large CO_2 exchanges were observed during the early-season drought in 2014 at the Grazed site (Fig. S3). This may be caused by 45 mm of precipitation before the growing season, which is two times higher the same period in 2015 and 2016. Furthermore, the average temperature was 19 °C and reached 26 °C a few days before the start of the 2014 drought experiment at the Grazed site (Fig. 1).

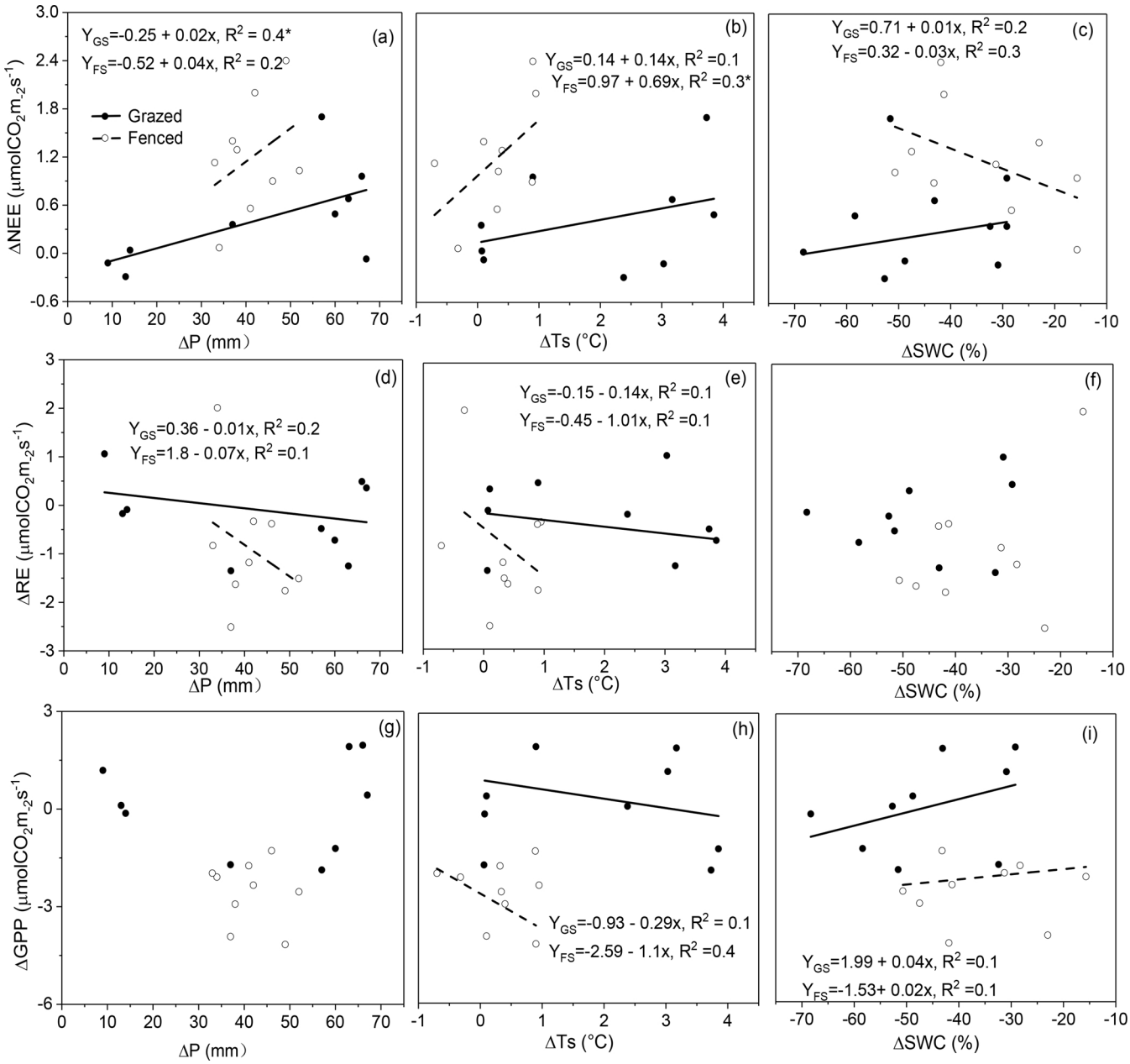

Fig. 5. Relationships of ΔNEE, ΔRE, ΔGPP (the difference in seasonal average NEE, RE, GPP between the drought and ambient treatments) with the removing precipitation amount (ΔP), the variations in soil water content (ΔSWC) and soil temperature (ΔTs) during three drought periods across three study years at the Grazed and Fenced site. ΔSWC and ΔTs is the difference of soil water content (0–20 cm depth of soil) and soil temperature (0–5 cm depth of soil) between drought period and the ambient. * means significant at $P \leq 0.05$.

The effect of extreme drought on ET was similar to the effects on CO_2 exchange during three study years in two sites, with an overall tendency of reduction (Fig. 3). Such similar response of CO_2 and water exchanges have been observed in previous studies (Bowling et al., 2010; Scott et al., 2015; Biederman et al., 2016).

4.2. Does seasonal timing of drought regulate its impacts on CO_2 and water exchanges?

Previous studies have shown that carbon and water exchanges are strongly regulated by the inter-seasonal timing of drought (e.g. spring vs. summer drought) (De Boeck et al., 2010; Wolf et al., 2016; Denton et al., 2017). Instead, we focused here on the intra-seasonal timing of drought within a growing season. At the Grazed site, early-season drought caused greater carbon and water losses than mid- and late-season drought, changing the ecosystem from carbon-neutral (i.e. NEE ≈ 0) to a net carbon source in two of three years (Fig. 3 and Table 2). One might assume that this could be attributed simply to the interactions of phenological factors and reduced SWC (Bowling et al., 2010; Zeiter et al., 2016). Alternatively, seasonal timing effects could be related to the different amounts of rainfall excluded as a function of seasonal rainfall distribution. Although the drought duration is the same for all three drought treatments, early-season drought excluded more rainfall as compared to the ambient condition than the other two treatments (29%–38% for DE, 8%–25% for DM and 4%–36% for DL. Table S1), due to seasonal rainfall patterns. The depletion of antecedent soil and high plant water demand in the early growing season could have caused fast soil drying in spite of lower leaf area of the plants (Cornelius et al., 2013). Photosynthesis inevitably declines when SWC falls below the wilting point (Resco et al., 2008). Furthermore, CO_2

Table 3
Summary of the relative effect of drought periods on CO_2 exchange (NEE, RE and GPP) determined by multiple regression analyses using precipitation amount (P) and soil water content (SWC) in the Grazed and Fenced sites. DE and DM indicate extreme drought events occurring at early- and mid-season stages. SE indicates standardized regression coefficient. Extreme drought occurring at late-season state (DL) was considered as reference dummy variable in the regression analysis.

Site	Regression equation	R^2	*P*	SE_{DE}	SE_{DM}
Grazed	NEE = 3.6-0.01 P-0.2SWC-0.2DE + 0.3DM	0.7	0.2	−0.2	0.2
	RE = -0.8 + 0.1 P + 0.01SWC + 0.4DE − 0.01DM	0.8	0.07	0.3	−0.01
	GPP = -4.5 + 0.3 P + 0.2SWC + 0.6DE − 0.3DM	0.7	0.2	0.2	−0.1
Fenced	NEE = -5.1-0.01 P + 0.4SWC-0.7DE-0.7DM	0.9	< 0.01	−1.2	−1.1
	RE = 2.7 + 0.01 P - 0.2SWC + 0.01DE + 0.05DM	0.7	0.2	0.01	0.03
	GPP = 6.0 + 0.02 P - 0.6SWC + 0.5DE + 2.4DM	0.5	0.5	0.2	0.04

exchange measurements showed incomplete recovery after early-season drought, which led to the ecosystem losing more carbon to the atmosphere at both sites (Fig. 4a).

Mid-season drought might be expected to have the most serious effects because leaf area is maximal and evaporative demand is at its peak (high vapor pressure deficits due to higher temperature). However, the Grazed site results do not support that expectation. One possibility is that mid-season drought treatment reduced rainfall, as compared to the ambient, by less than early-season drought, ranging from 8% to 25%. Importantly, mid-season ambient precipitation across three study years was less than the historical average for this period (Table S1). This implies that the ambient plots also suffered from water stress during the three years of the experiment, reducing the observed differences between the mid-season drought treatment and ambient plots. During the late growing season, average ambient rainfall is much lower (Table S1). Therefore, plants begin to senesce and assimilation declines, regardless of drought treatment. Low temperature and water availability in all plots, including ambient, may diminish the measurable treatment effects on water and CO_2 exchanges (Fig. S2 and Fig. 3a–c).

It is important to note that at the Fenced site, all three drought treatments decrease seasonal average CO_2 exchange during the growing

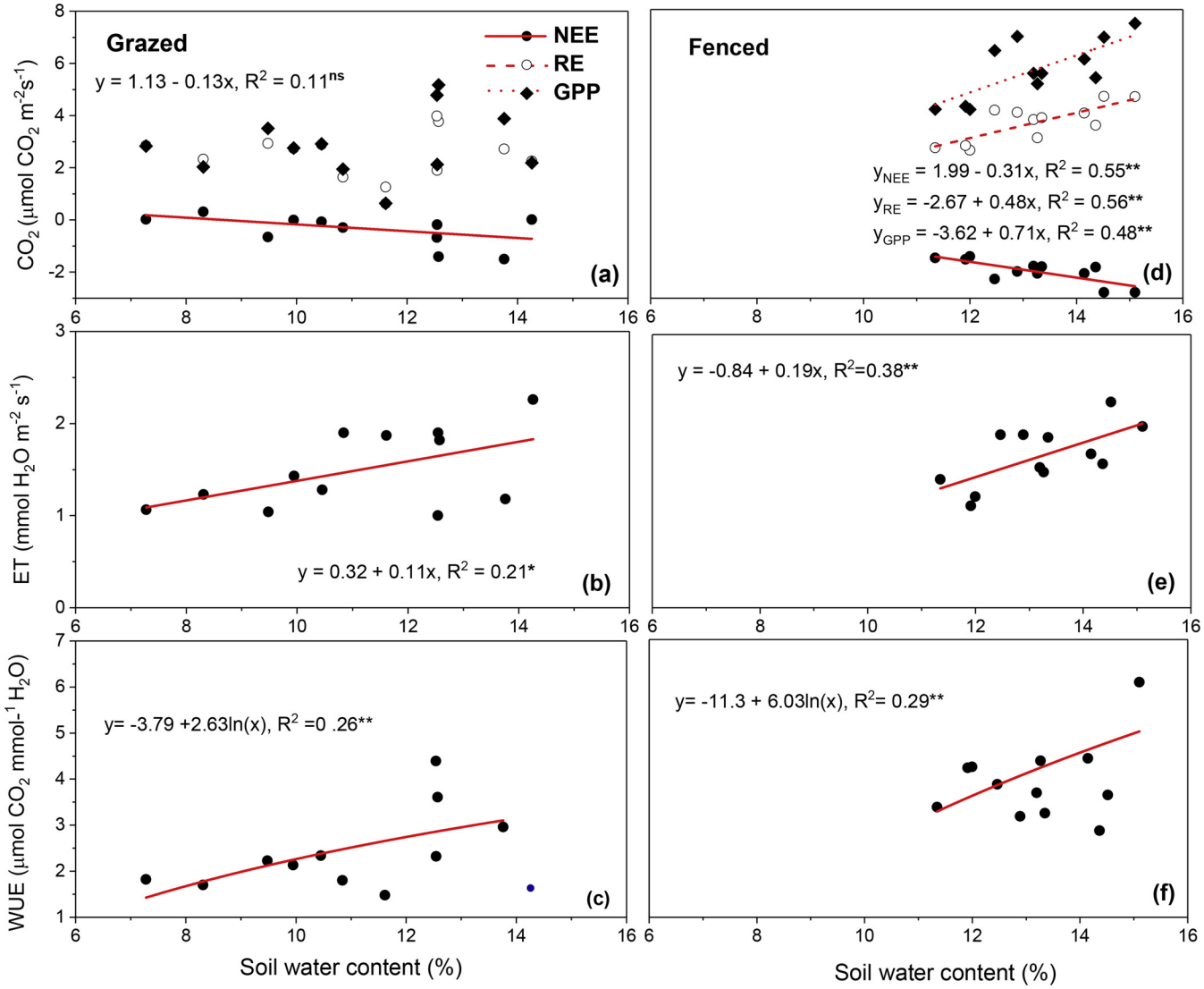

Fig. 6. Relationships of net ecosystem carbon exchange (NEE), gross ecosystem productivity (GPP), ecosystem respiration (RE), evapotranspiration (ET) and water use efficiency (WUE) with soil water content (SWC) across three study years. Dots represents the seasonal means of each plot at the (a–c) Grazed and (d–f) Fenced site.

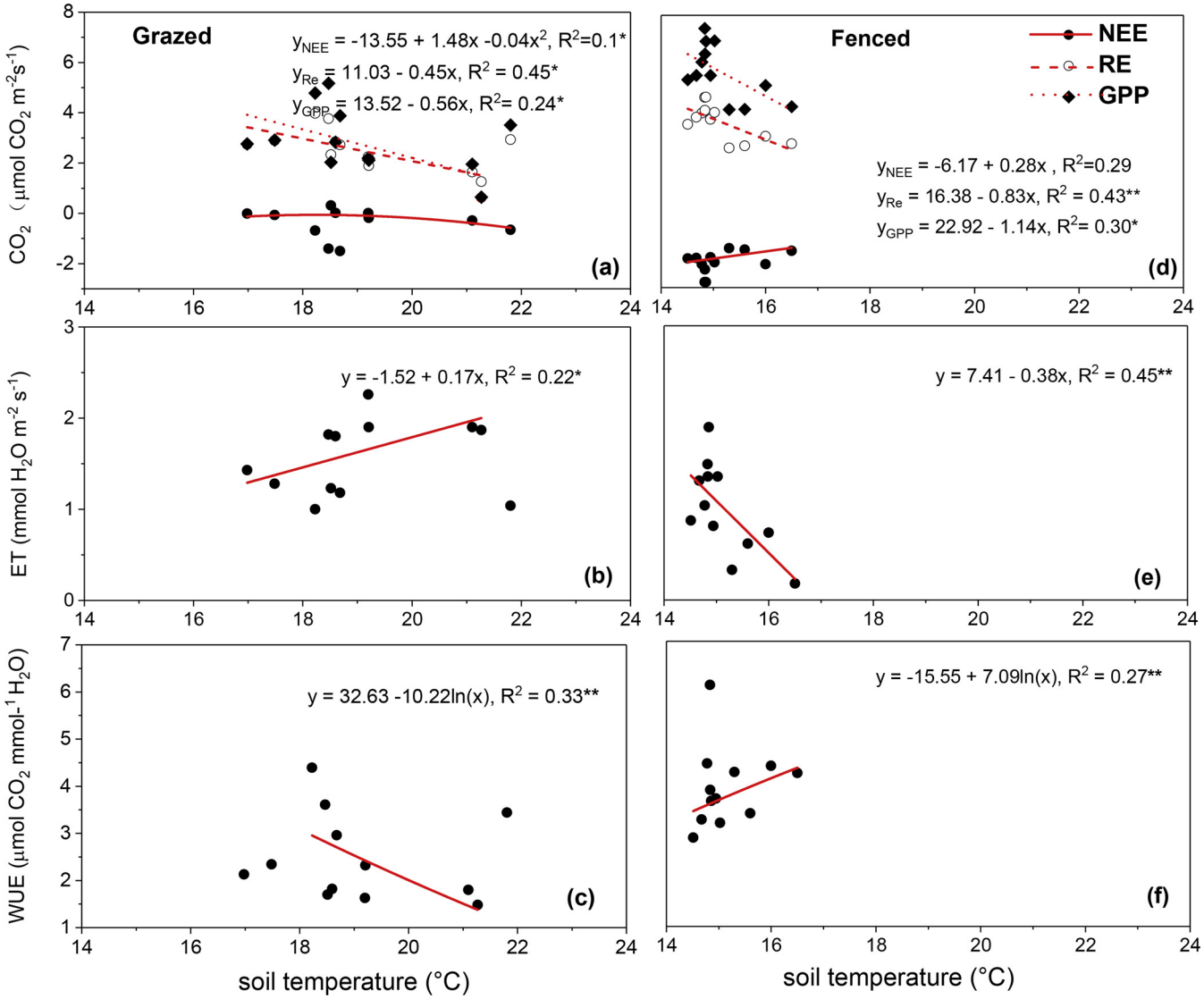
Grazed
y_{NEE} = -13.55 + 1.48x -0.04x^2, R^2=0.1*
y_{Re} = 11.03 - 0.45x, R^2 = 0.45*
y_{GPP} = 13.52 - 0.56x, R^2= 0.24*
(a)
Fenced
NEE
RE
GPP
y_{NEE} = -6.17 + 0.28x , R^2=0.29
y_{Re} = 16.38 - 0.83x, R^2 = 0.43**
y_{GPP} = 22.92 - 1.14x, R^2= 0.30*
(d)
CO_2 （μmol CO_2 $m^{-2}s^{-1}$)
y = -1.52 + 0.17x, R^2 = 0.22*
(b)
y = 7.41 - 0.38x, R^2 = 0.45**
(e)
ET (mmol H_2O m^{-2} s^{-1})
y = 32.63 -10.22ln(x), R^2 = 0.33**
(c)
y = -15.55 + 7.09ln(x), R^2 = 0.27**
(f)
WUE (μmol CO_2 mmol-^{1} H_2O)
soil temperature (°C)
soil temperature (°C)

Fig. 7. Relationships of net ecosystem carbon exchange (NEE), gross ecosystem productivity (GPP), ecosystem respiration (RE), evapotranspiration (ET) and water use efficiency (WUE) with soil temperature (Ts) across three study years. Dots represents the season means of each plot in the (a–c) grazed and (d–f) fenced site.

season (Fig. 3e–h). This suggests that although drought has negative effects on carbon uptake, timing of drought is not as important as drought itself in this long-term fenced steppe. Except for the above-mentioned reasons resulting in the reduction of net carbon uptake, long-term fence management led to much litter accumulation (ca. 350 g dry matter m^{-2}, as compared to negligible litter in the Grazed site). The loss of carbon through litter decomposition accounts for 30–50% of ecosystem respiration in this site (Wang et al., 2011). Hence litter decomposition may explain why seasonal timing of drought did not affect drought impacts on CO_2 exchange at the Fenced site.

4.3. Regulation of carbon and water exchange by soil temperature and moisture

Prior studies have shown that the responses of ecosystem CO_2 and water exchange to soil water content may be positive (Jia et al., 2016; Tian et al., 2016) or negative linear (Strack et al., 2009). The relationship between carbon exchange and soil temperature could be regulated by soil water content because soil microbial activity and plant growth can be regulated by water (Hao et al., 2008; Casals et al., 2011; Wang et al., 2014), consistent with our results (Fig. 6). The significant positive relationship between GPP, RE and SWC and negative relationship between NEE and SWC were observed at the Fenced site (Fig. 6b). However, at the Grazed site, we surprisingly found the variations in the gross fluxes GPP and RE did not depend on SWC, and the linear relationship between SWC and NEE was only marginally significant (P = 0.1, Fig. 6a). This result probably indicates that drought impacts on CO_2 exchange are regulated by interactions among the precipitation amount, soil temperature, and reduced SWC.

In terms of soil temperature, we found that at the Grazed site, GPP and RE have similar sensitivity to variations in Ts (Slope $_{GPP}$ = −0.56, R^2 = 0.24 and Slope $_{RE}$ = −0.45, R^2 = 0.45), while at the Fenced site, GPP showed greater temperature sensitivity than RE (Slope $_{GPP}$ = −1.14, R^2 = 0.24 and Slope $_{RE}$ = −0.83, R^2 = 0.45). At the Grazed site, the depth of surface soil is only 20–30 cm above a calcium-rich layer. However, a similar calcium layer occurred at 50 cm below the surface soil at the Fenced site. Together with higher evaporative demand (due to high temperature), these factors may have led to lower SWC at the Grazed site than Fenced site during the whole study period (Fig. 2 and Fig. S2). Therefore, increased Ts would synchronously decrease plant growth (i.e. stomatal closure and reduced assimilation) and RE (Selsted et al., 2012). This leads to the similar rate of change in GPP and RE with Ts change under the extreme drought conditions. At the Fenced site, we suggest that accumulation of litter results in lower

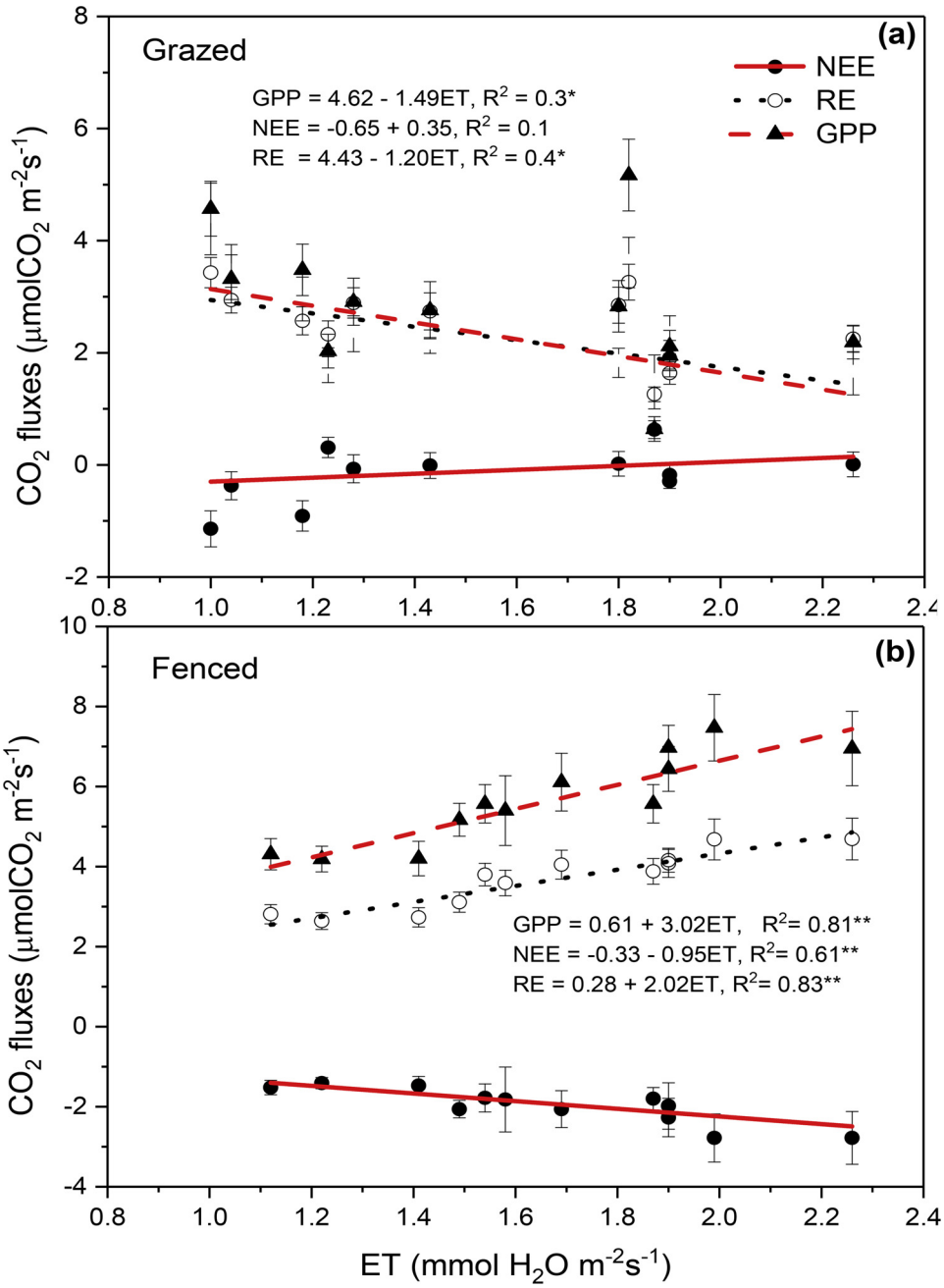
Grazed
(a)
NEE
RE
GPP
GPP = 4.62 - 1.49ET, R2 = 0.3*
NEE = -0.65 + 0.35, R2 = 0.1
RE = 4.43 - 1.20ET, R2 = 0.4*
Fenced
(b)
GPP = 0.61 + 3.02ET, R2= 0.81**
NEE = -0.33 - 0.95ET, R2= 0.61**
RE = 0.28 + 2.02ET, R2= 0.83**
CO2 fluxes (μmolCO2 m-2s-1)
ET (mmol H2O m-2s-1)

Fig. 8. Relationships among ecosystem CO_2 and water processes (evapotranspiration: ET) from 2014 to 2016 at the (a) Grazed and (b) Fenced site. Dots represents the season means of each plot.

fluctuating amplitude of Ts (14.5 °C–16.5 °C for the Fenced site, 15.5 °C–22.0 °C for the Grazed site) and higher SWC than the Grazed site due to litter attenuating incident radiation and soil water evaporation (Scarlett et al., 2017). RE is a combination of autotrophic respiration, which is dominated by plant maintenance respiration and more sensitive to temperature than water availability, and heterotrophic microbial respiration, which is regulated by soil nutrients, litter input, soil water and soil temperature (Balogh et al., 2015; Casals et al., 2011; Wang et al., 2013). Therefore, increased Ts would enhance autotrophic respiration and counteract the decrease in heterotrophic respiration induced by drought. This may explain the observed greater reduction in GPP than RE at the Fenced site.

4.4. Relationship between CO_2 and water exchanges under extreme drought

In the analysis of eddy covariance-based CO_2 and water exchanges in semi-arid sites, prior results showed that ET, representing water availability, predicts CO_2 exchange after hydrologic losses (Biederman et al., 2016, 2017; Jia et al., 2016). ET is a strong predictor of both gross and net CO_2 uptake and may also predict RE due to direct and indirect control of respiration by water (Xiao et al., 2013; Biederman et al., 2016, 2018). While our observations show that the variation in CO_2 exchange could be explained by ET under extreme drought stress (Fig. 8), the sign of the relationship was opposite at the Fenced and Grazed sites. As mentioned above, ET is composed of soil evaporation and plant transpiration. At the Grazed site it is likely that more evaporation, especially during the drought treatment, would dry the litter

and shallow soil layers critical to heterotrophic respiration (Reichstein et al., 2002; Hu et al., 2009). A slightly lower slope of RE to ET (−1.20) than GPP to ET (−1.49) builds upon the finding that NEE non-significantly increased with ET. However, at the Fenced site, where significant litter covers the soil, transpiration contributes most to ET (Huang et al., 2010). This suggests at the Grazed site, CO_2 exchange are probably regulated by controls other than water, while at the Fenced site, water supply is the main control.

Furthermore, a weak relationship between ET and NEE at the Grazed site implies that ET may be a good proxy for plant stomatal response to drought conditions (Fig. 8a). Increased ET leads to enhanced stomatal conductance and a concomitant increase of growth. Because studies have found autotrophic respiration is dominantly governed by recent photosynthesis, enhanced growth induced by plant transpiration caused high autotrophic respiration (Correia et al., 2012; Frank et al., 2015). As we did not separate respiration into autotrophic and heterotrophic respiration, we cannot convincingly determine whether increased transpiration with ET increase causes the heterotrophic respiration change. It is possible that plant growth enhances secretion of root exudates, which are respired by microbial and root-associated mycorrhizae and stimulate heterotrophic respiration (Raich and Schlesinger, 1992; Ortas et al., 2016).

Changes in WUE may be determined by different drought sensitivities of GPP and ET associated with dynamic variation of soil water and temperature (Hu et al., 2008; Xiao et al., 2013). Our findings at the Grazed site are aligned with previous studies in semi-arid areas showing increased water availability leads to enhanced WUE, possibly due to greater leaf area (Zhang et al., 2017; Scott and Biederman, 2017). It is worth noting that contrasting negative and positive relationships between WUE and Ts were observed at the Grazed and Fenced sites, respectively (Fig. 7c, f). This can be explained by the different sensitivities of GPP and ET to drought-induced changes in Ts (Fig. 6–7) as mentioned above. Therefore, our study suggests that WUE response to drought is related to the variations in SWC and Ts.

5. Conclusions

In conclusion, three extreme drought events (consecutive days without rainfall) respectively occurring during the early-, mid- and late-growing season equally decreased CO_2 and water exchange at a fenced steppe ecosystem. In contrast, at a grazed steppe ecosystem, extreme drought early in the growing season more strongly affected C cycling, particularly reducing net C uptake, than drought imposed in the middle to late growing season. The divergent responses observed in these two steppe management types underline the potential role of drought timing within the growing season in forecasting and modelling carbon cycle changes in the context of extreme climate events.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.agee.2018.06.010.

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